The distribution of seabirds and fish in relation to ocean currents in the southeastern Chukchi Sea

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Abstract

In late August 1988, we studied the distribution of seabirds in the southeastern Chukchi Sea, particularly in waters near a major seabird colony at Cape Thompson. Foraging areas were characterized using hydrographic data obtained from hydroacoustic surveys for fish. Murres (*Uria* spp.) and Black-legged Kittiwakes *Rissa tridactyla* breeding at Cape Thompson fed mostly on Arctic cod, which are known from previous studies to be the most abundant pelagic fish in the region. Our hydroacoustic surveys revealed that pelagic fish were distributed widely, but densities were estimated to be low (e.g., 0.1–10 g·m^{-3}) throughout the study area, and few schools were recorded. Large feeding flocks of murres and kittiwakes were observed over fish schools with densities estimated to exceed 15 g·m^{-3}. Fish densities were higher in shallow Alaska Coastal Current waters than offshore in Bering Sea waters, and most piscivorous seabirds foraged in coastal waters. Poor kittiwake breeding success and a low frequency of fish in murre and kittiwake stomachs in late August suggested that fish densities were marginal for sustaining breeding seabirds at that time. Planktivorous Least Auklets *Aethia pusilla* and Parakeet Auklets *Cyclorrhynchus psittacula* foraged almost exclusively in Bering Sea waters. Short-tailed Shearwaters *Puffinus tenuirostris* and Tufted Puffins *Fratercula cirrhata* foraged in transitional waters at the front between Coastal and Bering Sea currents.

Résumé

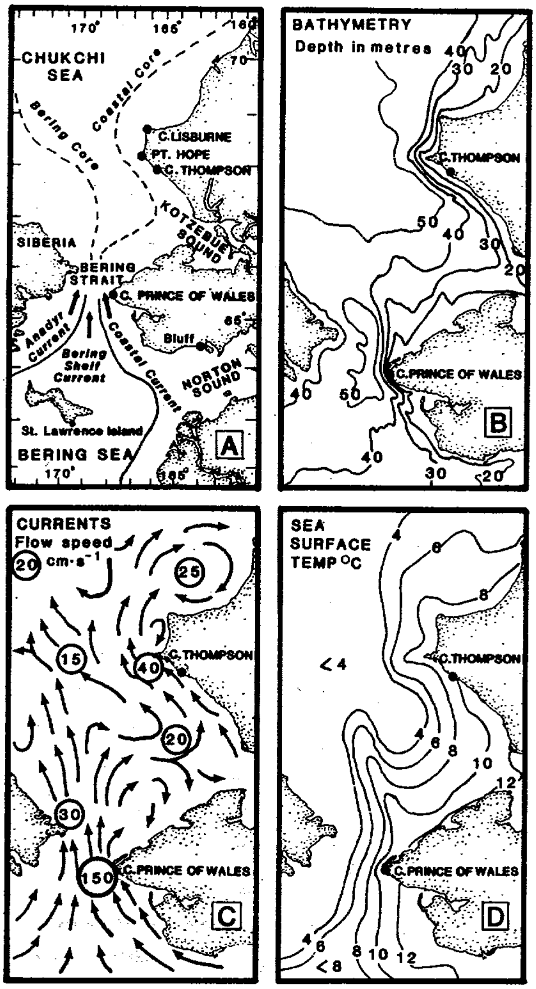
À la fin août 1988, nous avons étudié la distribution des oiseaux de mer dans le sud-est de la mer des Tchouktches, plus particulièrement à proximité d'une importante colonie de ces oiseaux au cap Thompson. Les caractéristiques des zones d'alimentation ont été déterminées à l'aide des données hydrographiques obtenues dans le cadre de sondages hydroacoustiques pour l'étude des poissons. Les marmettes *Uria* spp. et les Mouettes tridactyles *Rissa tridactyla* s'alimentant au cap Thompson se nourrissaient principalement de saïda franc qui, d'après des études antérieures, est le poisson pélagique le plus abondant dans la région. Nos sondages hydroacoustiques ont révélé que les poissons pélagiques sont très répandus, mais que leur densité est faible (0,1–10 g·m^{-3}) dans toute la zone d'étude; peu de bancs ont été observés. D'importants groupes de marmettes et de Mouettes tridactyles ont été aperçus au-dessus de bancs de poissons dont la densité estimée dépassait 15 g·m^{-3}. La densité des poissons était plus élevée dans les eaux peu profondes du courant côtier de l'Alaska qu'au large dans la mer de Béring, et la plupart des oiseaux de mer piscivores s'alimentaient dans les eaux côtières. Le faible succès de reproduction des Mouettes tridactyles et la fréquence peu élevée des poissons dans l'estomac de celles-ci ainsi que des mouettes à la fin août indiquent que la densité des poissons est alors un facteur marginal pour la survie des oiseaux de mer se reproduisant dans la région. L'Alque minuscule *Aethia pusilla* et l'Alque perroquet *Cyclorrhynchus psittacula*, qui sont des oiseaux planctivores, s'alimentaient presque exclusivement dans la mer de Béring. Les Puffins à bec mince *Puffinus tenuirostris* et les Macareux huppés *Fratercula cirrhata* s'alimentaient dans la zone de transition entre le courant côtier et le courant de la mer de Béring.

1. Introduction

The southeastern Chukchi Sea (Fig. 1) supports a large and diverse seabird fauna during summer. In the Bering Strait, about 1 million planktivorous Least Auklets *Aethia pusilla*, Crested Auklets *A. cristatella*, and Parakeet Auklets *Cyclorrhynchus psittacula*, and five other members of the Alcidae breed on Little Diomede Island and forage in locally productive waters and northwards into the Chukchi Sea (Drury et al. 1981). At Cape Thompson and Cape Lisburne on the northwest Alaska mainland, about 500 000 piscivorous seabirds, mainly Thick-billed Murres *Uria lomvia*, Common Murres *U. aalge*, and Black-legged Kittiwakes *Rissa tridactyla*, breed at colonies and forage locally on schooling pelagic fishes (Springer et al. 1984). Nonbreeding migrants, such as Short-tailed Shearwaters *Puffinus tenuirostris*, move through the Bering Strait into the Chukchi Sea in summer, whereas some terrestrially breeding species, notably phalaropes and jaegers, pass through the Chukchi Sea and forage en route to northern breeding grounds or southern wintering areas. In total, some 25 species of marine birds, including Tufted Puffins *Fratercula cirrhata*, Horned Puffins *F. corniculata*, and Glaucous Gulls *Larus hyperboreus*, regularly reside or forage in the southeastern Chukchi Sea during summer (Swartz 1967; Drury et al. 1981) (Appendix 1).

Productivity in the southeastern Chukchi Sea is elevated during summer and localized by several physical and biological mechanisms (Fleming and Heggarty 1966; Coachman et al. 1975; Springer et al. 1984). The dominant oceanographic feature of the region is the movement of three major currents north through the Bering Strait into

Figure 1
Oceanography of the southeast Bering Sea (adapted from Fleming and Heggarty 1966; Coachman et al. 1975). (A) Place names mentioned in text and major currents. (B) Bathymetric contours. (C) Current directions and flow speeds. (D) Generalized pattern of sea surface temperatures (adjusted with data collected in this study).



the Chukchi Sea (Fig. 1). The Alaska Coastal Current, characterized by warm, low-salinity water, blankets the nearshore zone as it constricts and surges north past Cape Prince of Wales, winds back to the southeast and broadens into Kotzebue Sound, and constricts again along the Alaska coastline from south of Cape Thompson to Cape Lisburne. Bering Shelf and Anadyr waters converge at the Bering Strait to form a core of cold, nutrient-rich, high-salinity Bering Sea water that dominates the south-central Chukchi, pushes eastward against the Alaska Coastal Current north of Kotzebue Sound to Point Hope, and traverses northwest towards the Arctic Ocean. Each current carries northward a unique mixture of nutrients, plankton, and fish that add to, and stimulate, all levels of production in the Chukchi Sea (Springer et al. 1984). Production is also enhanced through local mechanisms. Retreating Arctic ice in June and July provides ice-edge habitat for plankton growth and associated predators, particularly Arctic cod *Boreogadus saida*, the most abundant and widely distributed fish in the southeastern Chukchi Sea (Alverson and Wilimovsky 1966). Sandy substrates maintained nearshore by the Alaska Coastal Current provide habitat for sand lance *Ammodytes hexapterus*, and the warm nearshore waters stimulate growth and production of sand lance and other coastal fishes, including saffron cod *Eleginus gracilis*, herring *Clupea harengus*, and sculpins (Cottidae). Where the Alaska Coastal and Bering Sea currents border, fronts may stimulate local production (Springer et al. 1984).

The main purpose of our study was to determine where breeding birds from colonies at Cape Thompson were foraging in late August 1988 and to identify factors influencing the distribution of seabirds (including nonbreeders and migrants) in the southeastern Chukchi Sea. Data were also collected on seabird and fish distributions around Cape Lisburne and the Diomede Islands. Hydroacoustic surveys for fish were conducted simultaneously with bird surveys to measure the density and distribution of potential prey. Seawater temperature and salinity were measured to characterize water masses and foraging habitats. We collected data on breeding success, diet, and body condition of murres and kittiwakes breeding at Cape Thompson, and we interpret these data in light of information gathered on pelagic fish and bird distributions and from previous studies.

2. Methods

Surveys for seabirds were conducted in the southeastern Chukchi Sea from 23 to 28 August 1988 from the U.S. Fish and Wildlife Service vessel MV 'Tiglax.' Moderate to strong northeasterly winds prevailed throughout the study and limited the collection and interpretation of some data (see below). Except where noted otherwise, seabird censuses were conducted over 10-min intervals from the flying bridge of the MV 'Tiglax' using standard methods for recording species abundance and behaviour (Gould and Forsell 1989). Exact protocols varied depending on the type of survey being conducted (Table 1). When hydroacoustic surveys for fish were conducted simultaneously with bird observations, all birds were counted in a 300-m-wide strip directly in front of the vessel, and the exact time within the census period that birds on the water were observed was noted (except for survey Nos. 1 and 2, in which the strip width was reduced to 150 m, birds were counted over 2-min intervals, and only birds on the water were recorded). Otherwise, all birds were counted in a 300-m-wide strip to the left or right of the ship's centre line, depending on which side offered better viewing conditions (Gould and Forsell 1989). Four of 11 surveys were conducted as arcs around the breeding colonies at Cape Thompson and Cape Lisburne (Table 1, Fig. 2) to determine the directions taken by birds flying to foraging areas. Only flying murres were counted on the first of these arcs (survey No. 4) because of poor lighting conditions, and censuses were conducted over 5-min intervals on other arcs.

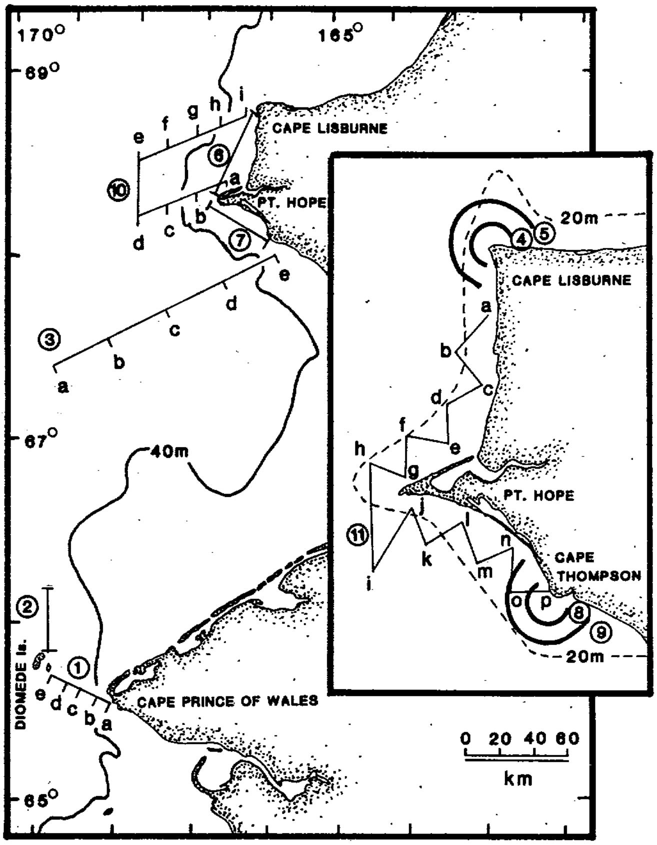
On all surveys, sea surface (3 m depth) temperatures (SST) and salinities (SSS) were monitored using a continuously recording thermosalinograph (Tsurumi Seiki Model 305861, Yokogawa Hokushin Electric Co.). On survey Nos. 1, 3, and 10, water temperature profiles were obtained at the indicated stations (Fig. 2) using a conductivity–temperature–depth (CTD) recorder (Tsurumi Seiki Model 01930 In-situ Water Quality Monitor, Tsurumi Seiki Company Ltd., Yokohama, Japan). The CTD was calibrated in fixed salinity and temperature baths, and the thermosalinograph was calibrated from CTD measurements at 3 m. Additional information on wind speed and direction, sea state, observation conditions, and position

Table 1
Numbers and densities of seabirds observed on surveys in the southeastern Chukchi Sea in August 1988

Survey No.	Date	Survey period[a]	Area (km²)	All birds No.	All birds No./km²	Birds on water No.	Birds on water No./km²	Survey type[b]
1	23 Aug.	1425–1845	8.0	—	—	58	7.3	I, H
2	23 Aug.	2140–2340	7.4	—	—	17	2.3	O, H
3	24 Aug.	0725–1555	42.6	452	10.6	27	0.63	O
4	24 Aug.	1025–1135	6.5	570	87.7	—	—	I, A
5	25 Aug.	0815–1020	11.6	2 033	175.3	16	1.4	I, A
6	25 Aug.	1045–1315	13.9	675	48.6	55	4.0	I
7	25 Aug.	1915–2130	12.5	584	46.7	20	1.6	I
8	26 Aug.	1310–1425	6.9	695	100.7	11	1.6	I, A
9	26 Aug.	1505–1650	9.7	1 394	143.7	24	2.5	I, A
10	27 Aug.	0830–1900	49.9	1 450	29.1	77	1.5	O, H
11	28 Aug.	0840–1840	55.5	3 874	69.8	650	11.7	I, H
Total or mean			224.5	11 802	53.7[c]	955	9.0	

[a] Survey period indicates time from beginning to end of survey, including stops for CTD casts. Ship speed varied with sea state.
[b] I = inshore, O = offshore, A = arc around colony, H = hydroacoustic survey conducted simultaneously.
[c] Arcs around colonies excluded from calculation.

Figure 2
Surveys conducted in the southeastern Chukchi Sea in August 1988. Numbers in circles indicate survey number (see Table 1). Lower-case letters along survey Nos. 1, 3, and 10 indicate location of CTD stations; those along survey No. 11 (inset) indicate location of waypoints.



were noted at the beginning of each census period (Gould and Forsell 1989).

Hydroacoustic surveys were conducted using a BIOSONICS Model 102 Echosounder and a hull-mounted 120-kHz dual-beam transducer (4 m below the surface). Transmit power was set at 217 dB, gain at −125.4 dB, bandwidth at 5 kHz, trigger interval at 0.5 s, and pulse width at 0.5 ms for all surveys. Fish echo signals were integrated in real time over 2-min time intervals and 10-m depth intervals using a BIOSONICS Model 121 Digital Echo Integrator with 20 LogR amplification. Integration thresholds were set at 100 mV for each depth stratum. Signals were integrated in relative voltage units, downloaded onto a microcomputer, and later converted to estimates of fish density and abundance. Integrations of echo signals in the upper 10 m of the water column were not used to calculate fish densities because rough seas introduced air bubbles into the water column and produced excessive surface noise most of the time.

Assuming that Arctic cod were the most abundant fish in the area (Alverson and Wilimovsky 1966) and using the average size of Arctic cod consumed by seabirds at Cape Thompson (see Results), we used a target strength of $-64\ dB{\cdot}g^{-1}$, calculated from regression equations for fish with closed swimbladders (physoclists), to estimate absolute from relative fish densities (Thorne 1983; Foote 1987). In situ measurements of Arctic cod target strengths in Lancaster Sound indicate that this is a good estimate (R. Crawford, pers. commun., Fisheries and Oceans Canada, Winnipeg), and it is very close to target strengths determined in situ for capelin *Mallotus villosus* and Atlantic cod *Gadus morhua* in eastern Canada (Rose and Leggett 1988; D. Miller, pers. commun., Fisheries and Oceans Canada, St. John's). In the absence of trawl samples to identify and measure fish targets, however, the fish densities presented here must be considered approximate. One other forage fish likely to have been encountered in August was sand lance (Springer et al. 1984). There are no published estimates for sand lance target strengths, but because they have "open" swimbladders (physostomes), it is likely that target strengths are about 5–10 dB lower than those of cod and capelin (Foote 1987; Rose and Leggett 1988). This would lead to an underestimate of fish densities where sand lance were recorded (only nearshore) (Alverson and Wilimovsky 1966; Springer et al. 1984). Another potential source of error was the inclusion of zooplankton signals in echo integrations. However, zooplankton have much lower target strengths than fish (e.g., −80 to −100 dB) and, with the integration (noise) threshold set at 100 mV, would have made a negligible contribution to integration values (Greenlaw 1979). Faint zooplankton scattering layers were recorded on echograms, however, with the chart recorder threshold set at 30–50 mV.

We collected murres and kittiwakes for diet studies by shooting them as they returned to the colony. Birds were weighed, and the amount of subcutaneous and mesenteric fat was estimated visually (scale 0–3) (Gaston et al. 1983). Stomachs and gizzards were removed and stored in 50% ethanol solution for later examination. Stomach contents were sorted and identified in the laboratory using appropriate taxonomic keys and reference material (A. Springer, Institute of Marine Science, University of Alaska, Fairbanks). The sizes of most fish prey recovered were reconstructed from regressions of fish length on otolith length and of fish weight on fish length (for details, see Springer et al. 1984).

The measurement of fish and seabird aggregations, and correlations between them, depends on the spatial scale at which data are collected and analyzed (Schneider and Piatt 1986; Piatt 1990). Therefore, correlations were examined over a range of scales, from the minimum measurement scale (i.e., 2, 5, or 10 min, depending on the survey, where time is equivalent to distance traveled: e.g., 1 min = 0.3 km at a ship speed of 10 kn) to larger scales (i.e., 10, 20, 40, or 80 min, depending on the total survey length, with at least four data points for measuring correlations). Correlations between fish or birds and gradients in SST or SSS were similarly examined. Gradients were calculated by lagging temperature or salinity measurements by one measurement interval (e.g., 10 min) and taking the absolute value of the difference between successive observations as the gradient. Correlations between birds, fish, and gradients were measured at equivalent scales using Spearman rank correlation.

The affinity of different seabird species for different water types was examined by grouping 10-min bird observations according to whether they occurred in Bering Sea/Anadyr water (SST < 7.5°C, SSS > 31‰), transitional water (SST ≥ 7.5°C, SSS > 30‰), or Alaska Coastal water (SST ≥ 8.0°C, SSS < 30‰) as determined by the continuously recording thermosalinograph. The categorization of Bering Sea/Anadyr and Alaska Coastal water types by sea surface characteristics is based on definitions in Coachman et al. (1975), which differ from definitions based on CTD profiles of the entire water column because surface waters are warmer and less saline than underlying water. Our boundaries on the "transitional" water type are fairly arbitrary, however, and by definition represent the type of water found in mixed frontal zones between the well-defined Alaska Coastal and Bering Sea currents. Flying birds from arc and inshore surveys near Cape Thompson were excluded from this analysis, because those birds could have been flying over Coastal waters to get to foraging areas offshore.

3. Results

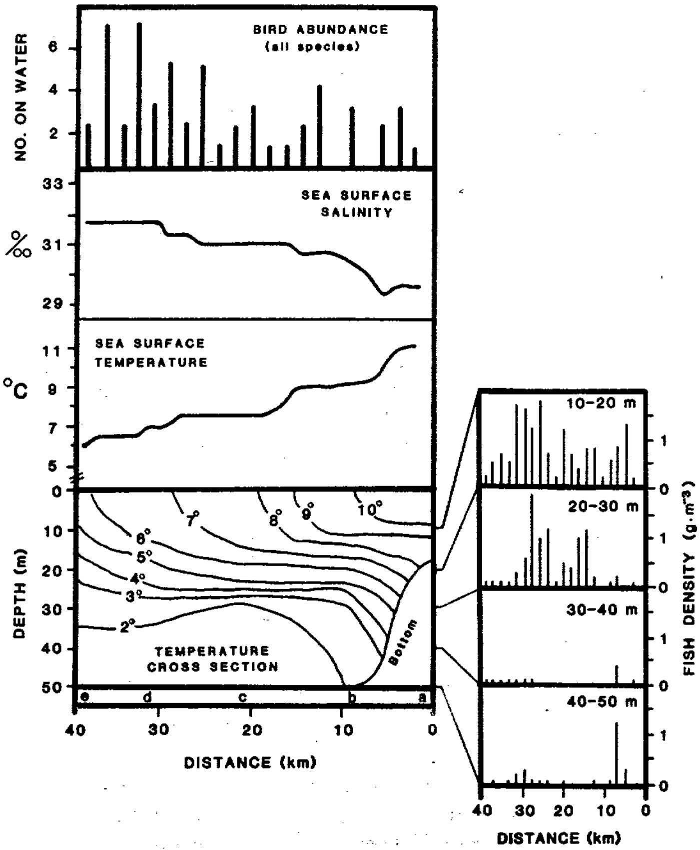
3.1. Bering Strait

On survey No. 1, we crossed the strait from Cape Prince of Wales to Little Diomede Island (Fig. 2). Thermosalinograph and CTD profiles revealed a marked temperature–salinity gradient from east to west and a thermocline at a depth of about 30 m (Fig. 3). Zooplankton were concentrated just above the thermocline, and estimated fish densities of up to about 2 g·m^{-3} were recorded in the 10–30-m layer. The density of birds on the water during this survey was higher than densities observed on all subsequent surveys except for coastal survey No. 11 at Cape Thompson (Table 1). In decreasing order of abundance, Parakeet Auklets, Common Murres, Tufted Puffins, and Glaucous Gulls accounted for 74% of birds observed on the water.

At the minimum measurement scale of 0.36 km and over larger scales (up to 9 km), there were no significant correlations between total birds and fish densities in any depth stratum. The surface layer (5–10 m) was excluded from this and subsequent analyses because surface signals were due to air bubbles introduced by turbulence, not to fish echoes. The "density" of signals in the uppermost stratum was significantly correlated with wind speed ($r = 0.85$, $n = 20$, $P < 0.0001$) and sea state ($r = 0.77$, $n = 20$, $P < 0.0001$).

On the survey north from Little Diomede Island (survey No. 2, Fig. 2), there was little variation in SST (6–8°C) or SSS (30.6–31.3‰) from beginning to end. Average fish densities were between 0.04 and 0.15 g·m^{-3} in the 10–40-m depth strata. Few birds were observed, of which 75% were Least, Parakeet, and Crested auklets. Most auklets were observed within 10 km of Little Diomede Island.

Figure 3
Observations of seabirds, fish, and hydrography on survey No. 1 across the Bering Strait. Lower-case letters at bottom correspond to CTD stations shown in Figure 2. Histogram at lower right shows fish densities at different 10-m depth strata along the survey track.



3.2. Crossing the southeastern Chukchi Sea

We crossed the southeastern Chukchi Sea from about 150 km west–southwest to about 10 km south of Cape Thompson (Fig. 2). Thermosalinograph and CTD profiles revealed that the survey started in the tongue of Alaska Coastal water that extends about 200 km north of Bering Strait (Fig. 1), crossed the broad band (approximately 80 km) of stratified Bering Sea water that intrudes towards Kotzebue Sound, and ended in the Alaska Coastal Current (about 50 km wide). Fronts between Alaska Coastal and Bering Sea waters, defined by large SST and SSS gradients and vertically mixed waters (Coachman et al. 1975), were observed at distances of 10–20 and 100–110 km along the survey track (Fig. 4). Hydroacoustic surveys were not conducted because of rough seas. Only 6% of birds observed were on the water, and the density of flying birds was lower than on any other survey (Table 1).

Nonetheless, some patterns were evident. Most Parakeet Auklets were observed at a front between Alaska Coastal and Bering Sea waters. Most phalaropes (of which 78% were identified as Red Phalaropes *Phalaropus fulicaria*) and Least Auklets were found over stratified Bering Sea waters. Murres were most abundant in Alaska Coastal waters within about 60 km of Cape Thompson. No significant correlations between birds and temperature–salinity gradients were found.

3.3. Radial arcs around Cape Thompson and Cape Lisburne

Radial surveys around Cape Thompson revealed that most murres and kittiwakes were flying to the

Figure 4
Observations of seabirds and hydrography on survey No. 3 across the southeastern Chukchi Sea. Lower-case letters at bottom correspond to CTD stations shown in Figure 2.

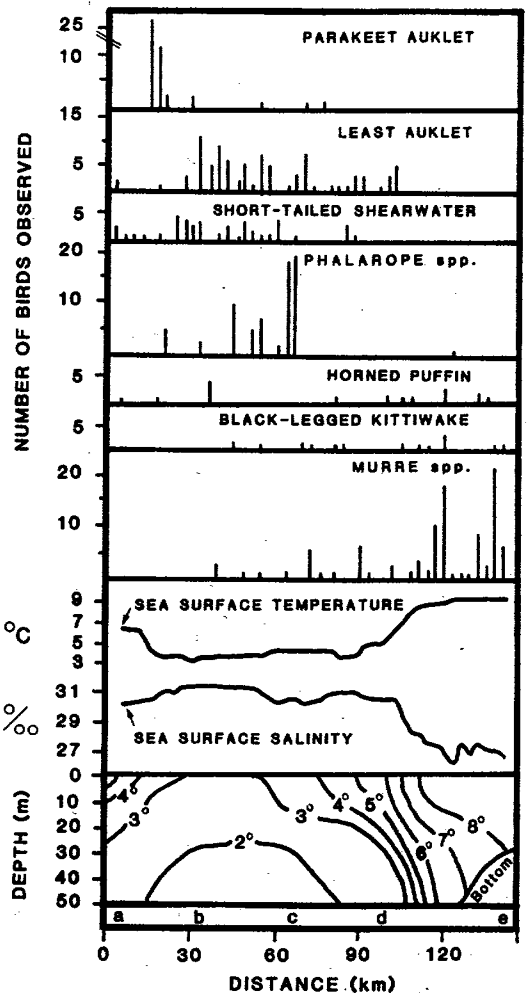
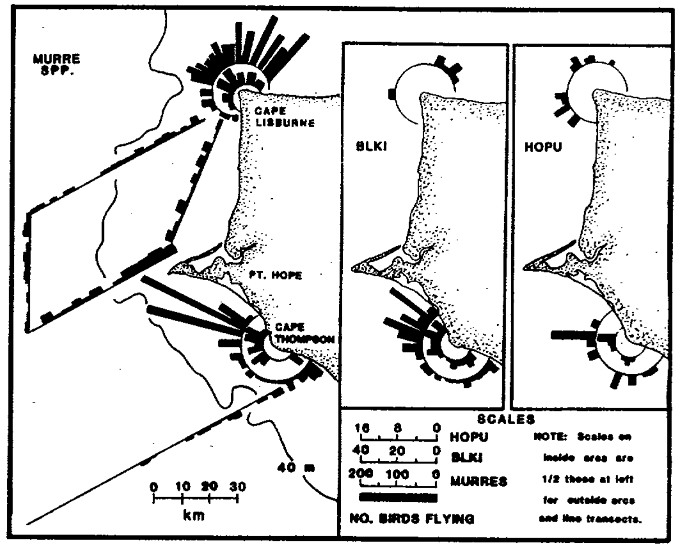


Figure 5
Murre, kittiwake (BLKI), and Horned Puffin (HOPU) flight directions from Cape Thompson and Cape Lisburne as determined from arc surveys around the colonies. Numbers of murres flying on offshore surveys (Nos. 3 and 10) are also shown.



northwest on 26 August and that a small proportion were flying southeast along the coast (Fig. 5). Horned Puffins flew mostly to the west and south of Cape Thompson. Surveys around Cape Lisburne revealed that most murres and kittiwakes flew to the northwest, north, and especially northeast. Again, Horned Puffins flew to different foraging areas than did murres and kittiwakes.

3.4. Offshore from Point Hope to Cape Lisburne

With evidence from the radial arc surveys and two coastal surveys (Nos. 6 and 7) that most birds from Cape Thompson were flying to the west and north of Point Hope, we conducted a survey (No. 10) to encompass potential foraging areas up to about 90 km west and 110 km northwest of Cape Thompson (Fig. 2). Thermosalinograph and CTD profiles revealed that the Alaska Coastal Current was constricted to a narrow band about 30 km wide off Point Hope (Fig. 6, CTD stations a–d) and was broader (about 40 km) off Cape Lisburne (Fig. 6, CTD stations e–i). SST and SSS gradients were stronger at the front between Alaska Coastal and Bering Sea waters off Point Hope than off Cape Lisburne.

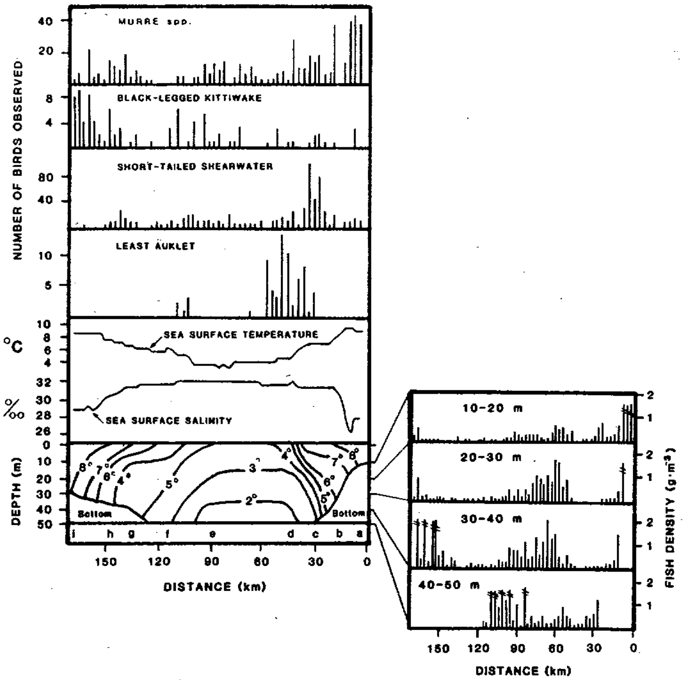
Fish density and distribution varied markedly between water masses (Fig. 6). In shallow, stratified Alaska Coastal waters at Point Hope, estimated fish densities were relatively high (up to 23 $g{\cdot}m^{-3}$), and most fish were distributed near the bottom or in midwater. Average fish density was estimated to be 1.6 $g{\cdot}m^{-3}$, and total fish biomass was estimated to be 35.5 $mt{\cdot}km^{-2}$. Moving offshore into the vertically mixed transitional waters between Alaska Coastal and Bering Sea waters (about 10 km on either side of CTD station c, Figs. 2 and 6), fish were conspicuously absent. Further offshore in stratified Bering Sea water, and moving north between CTD stations d and e, moderate fish densities (1–2 $g{\cdot}m^{-3}$) were recorded at depths of 20–40 m. In transitional and Bering Sea waters, estimated fish densities averaged 0.073 $g{\cdot}m^{-3}$, and fish biomass in the 10–40-m strata was estimated to be 2.19 $mt{\cdot}km^{-2}$. Upon returning inshore to Cape Lisburne (CTD stations e–i), estimated fish densities declined again dramatically in transitional waters (between CTD stations f and g) before rising again to much higher levels (up to 249 $g{\cdot}m^{-3}$) near the bottom in Alaska Coastal waters. Estimated fish densities in this area averaged 1.26 $g{\cdot}m^{-3}$, and total biomass was estimated to be 11.5 $mt{\cdot}km^{-2}$ in the 10–40-m strata.

At a 6-km spatial scale, there was a significant negative correlation between fish density and SST gradients in two of four depth strata examined (20–30 m: $r = -0.45$, $n = 28$, $P = 0.02$; 30–40 m: $r = -0.45$, $n = 28$, $P = 0.02$). Negative correlations between fish density and SSS gradients were generally weaker and insignificant (except for the 20–30-m stratum: $r = -0.40$, $n = 28$, $P = 0.03$). This analysis corroborates the visual impression of Figure 6 that fish were scarce in the front between Alaska Coastal and Bering Sea currents.

At a spatial scale of 6 km, murres on the water (3% of total observed) were strongly correlated with fish density in the 10–20-m stratum ($r = 0.82$, $n = 28$, $P = 0.0008$) and the 10–30-m strata ($r = 0.60$, $n = 28$, $P = 0.03$). Reflecting the negative relationship between fish density and SST gradients, the number of murres on the water was also negatively correlated with SST gradients ($r = -0.79$, $n = 28$, $P = 0.04$) at a 6-km spatial scale.

Kittiwakes were not correlated with fish density in any depth stratum at any spatial scale. Only one kittiwake was observed on the water, and no feeding flocks were

Figure 6
Observations of seabirds, fish, and hydrography on survey No. 10 northwest of Cape Thompson. Lower-case letters at bottom correspond to CTD stations shown in Figure 2. Histogram at lower right shows fish densities in different 10-m depth strata along the survey track (broken bars indicate density values exceeding 2 g·m^{-3}, with values of 3–4 g·m^{-3} in the 10–20-m stratum; 23 g·m^{-3} in the 20–30-m stratum; 12–249 g·m^{-3} in the 30–40-m stratum; 4–80 g·m^{-3} in the 40–50-m stratum).



observed, however, so it was impossible to identify birds that were potentially foraging for this analysis. Like murres, however, kittiwakes were negatively correlated with SST gradients at both small (3 km: r = -0.38, n = 56, P = 0.03) and large (18 km: r = -0.90, n = 9, P = 0.04) spatial scales. Most kittiwakes were observed on approach to Cape Lisburne (Fig. 6), and the arc surveys (Fig. 5) suggest that those kittiwakes came from Cape Thompson rather than Cape Lisburne.

The only other seabirds seen in abundance were Short-tailed Shearwaters and Least Auklets. In contrast to murres, shearwaters and auklets were negatively correlated with fish abundance in most depth strata at a 6-km scale, although correlations were significant with fish only in the 30–50-m strata (auklet: r = -0.49, n = 24, P = 0.05; shearwater: r = -0.58, n = 24, P = 0.009). Most (81%) of the Least Auklets observed were swimming and were found on the Bering Sea side of the front between the Alaska Coastal and Bering Sea currents (Fig. 6). In contrast to murres and kittiwakes, Least Auklet numbers were positively correlated with SST gradients (r = 0.78, n = 28, P = 0.02) and SSS gradients (r = 0.83, n = 28, P = 0.04) at a 6-km spatial scale. All the shearwaters observed were flying; although they were dispersed over a wide area, the largest aggregations were found on the Alaska Coastal Current side of the front (Fig. 6). Shearwater numbers were not well correlated with property gradients.

3.5. Coastal survey

On 27 August and about 80 km south of Cape Lisburne, we encountered the first of only three large murre and kittiwake feeding aggregations observed during the study. About 4 km from shore, we passed over a small, dense school of fish on which about 500–700 murres, 25 kittiwakes, and 10 Glaucous Gulls were actively feeding. The echogram trace of this school was qualitatively different from all previous fish traces and similar to traces of known sand lance schools recorded in the Aleutians in the summer of 1988 (JFP, unpubl. data). On 28 August, we surveyed the shallow nearshore zone in a zigzag pattern from about 30 km south of Cape Lisburne to Cape Thompson (Fig. 2).

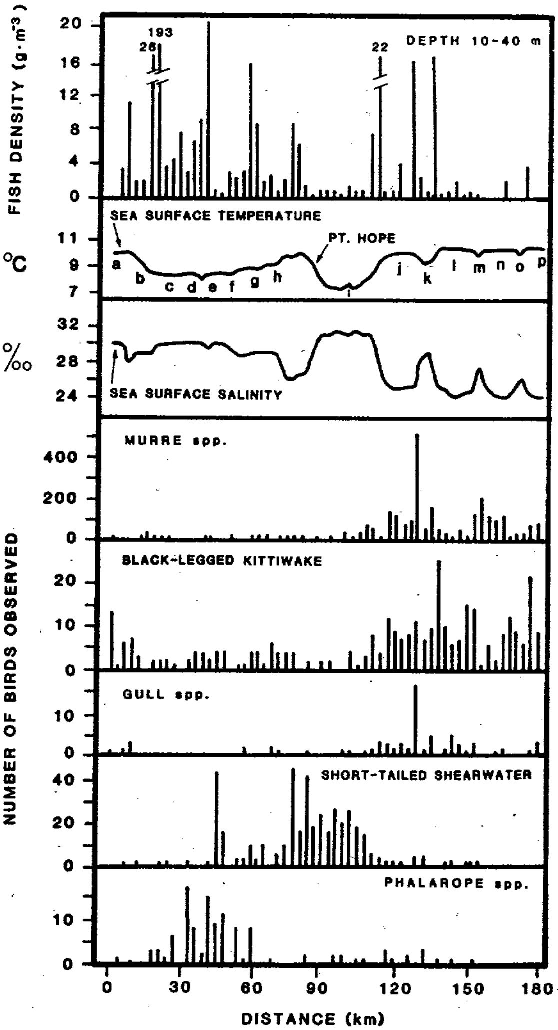
Thermosalinograph records indicated that north of Point Hope (waypoints a–h, Fig. 7), waters within the 20-m bathymetric contour (Fig. 2) were a nonhomogeneous mix of Alaska Coastal water and transitional or Bering Sea water. Alaska Coastal water predominated as we rounded Point Hope (after waypoint h), where temperatures increased and salinities decreased rapidly. Immediately south of Point Hope, cold, high-salinity transitional water predominated beyond the 20-m contour (waypoint i) and bordered (waypoints k, m, and o) with Alaska Coastal waters along the 20-m contour all the way to Cape Thompson. These observations are consistent with previous oceanographic studies of the area (Coachman et al. 1975): the Alaska Coastal Current is compressed by the Bering Sea Current as both traverse north past Point Hope, with greater mixing of the two water masses in a gyre north of Point Hope.

In the 10–20-m stratum, fish density was not correlated with SST or SSS gradients at any spatial scale. In the 20–30-m stratum, where the densest fish aggregations were found both north and south of Point Hope, fish density was positively correlated with SST gradients at a spatial scale of 3 km (r = 0.36, n = 62, P = 0.01). In the 30–40-m stratum, fish density was positively correlated with SST and SSS gradients at all spatial scales but reached a maximum at a scale of 12 km (SST: r = 0.69, n = 15, P = 0.01; SSS: r = 0.78, n = 15, P = 0.0009). Fish schools were densest on the coastal side of the border between Alaska Coastal and transitional waters, where temperatures and salinities changed rapidly, and were largely absent in the cold core of transitional water off Point Hope (waypoint i).

Over the whole survey area, estimated fish densities averaged 0.59 g·m^{-3}, and total biomass was estimated to be 5.3 mt·km^{-2} in the 10–30-m strata. However, fish densities north of Point Hope were generally higher over a larger area (estimated average density of 1.3 g·m^{-3}) than south of Point Hope (0.18 g·m^{-3}). North of Point Hope, at least five aggregations with densities greater than 10 g·m^{-3} and one school with a density of 193 g·m^{-3} were encountered (Fig. 7). No significant seabird feeding aggregations (i.e., more than five birds in a flock on the water) were found north of Point Hope. South of Point Hope, however, one large aggregation of murres (466), kittiwakes (10), and Glaucous Gulls (15) was found feeding actively on a school of fish that ranged from the surface to the bottom and had a maximum density of 14.3 g·m^{-3} in the 20–30-m stratum. From the echogram trace, this appeared to be a school of sand lance. If so, calculated densities would be higher (i.e., 70–140 g·m^{-3}), because sand lance have a lower target strength than most other fish likely to be encountered inshore (see Methods). One other seabird aggregation (41 murres, three kittiwakes, three gulls) was observed on the water above a similar school with densities of 16.5 g·m^{-3}.

It appeared that, with the exceptions noted above, many dense fish aggregations were not exploited by foraging seabirds (Fig. 7). Nonetheless, murres on the water (20% of 2922 birds) were significantly correlated with fish

Figure 7
Observations of seabirds, fish, and hydrography on coastal survey No. 11 north of Cape Thompson. Lower-case letters along sea surface temperature profile correspond to waypoints shown in Figure 2. Histogram at top shows fish densities summed over 10–40-m depth strata.



density in the 20–30-m stratum at intermediate spatial scales (12 km: r = 0.54, n = 15, P = 0.02). Similarly, kittiwakes on the water (6% of 326) were positively correlated with fish in the 20–30-m stratum at the same scale (r = 0.71, n = 15, P = 0.002). Murres were not correlated with temperature–salinity gradients at any spatial scale, and kittiwakes were weakly correlated with SST gradients at a 3-km scale (r = 0.27, n = 62, P = 0.04).

Most identified gulls were Glaucous Gulls, and their numbers were not correlated with fish densities. Like kittiwakes, however, gulls on the water (32% of 72 birds) were weakly correlated with SST (r = 0.27, n = 62, P = 0.04) and SSS (r = 0.34, n = 62, P = 0.01) gradients at the minimum spatial scale of 3 km. As expected from their distributions, neither shearwaters nor phalaropes were correlated with fish densities. Shearwaters were positively correlated with temperature gradients at intermediate spatial scales (6 km: r = 0.40, n = 31, P = 0.03; 12 km: r = 0.53, n = 15, P = 0.04). In marked contrast to murres and kittiwakes, shearwaters were concentrated in transitional waters off Point Hope (Fig. 7). In contrast to all other species, phalaropes (only Red Phalarope identified) were concentrated in an area just north of Point Hope (Fig. 7).

3.6. Summary: seabird affinities with water types

Numbers of the most abundant species observed during 10-min intervals on all surveys were superimposed on sea surface temperature–salinity diagrams to assess not only what water types were frequented by those species, but also where the largest aggregations occurred (Fig. 8). For example, whereas Short-tailed Shearwaters were widely distributed over all water types, many of the largest aggregations were found in transitional waters. Similarly, the largest kittiwake and Common Murre aggregations were located in Coastal waters. Thick-billed Murres were found in all water types. Least Auklets were restricted almost entirely to Bering Sea and transitional waters, and the largest aggregations were observed in high-salinity, low-temperature Bering/Anadyr water.

Using data adjusted for survey effort in each water type, we assessed the affinity of common species for each water type (Fig. 9) by testing (Chi-square) the hypothesis that birds were equally distributed among water types. This hypothesis was rejected for all species except Tufted Puffin (STSH χ^2 = 156.1, P < 0.0001; COMU χ^2 = 69.4, P < 0.0001; TBMU χ^2 = 38.7, P < 0.0001; TUPU χ^2 = 1.17, ns; HOPU χ^2 = 12.0, P = 0.002; LEAU χ^2 = 67.7, P < 0.0001; PAAU χ^2 = 12.5, P = 0.002; BLKI χ^2 = 39.4, P < 0.0001; GULL χ^2 = 63.8, P < 0.0001; PHAL χ^2 = 101.8, P < 0.0001; df = 2 in all cases). Birds with an affinity for Coastal waters included both murres, Horned Puffins, kittiwakes, gulls, and phalaropes (Fig. 9). Short-tailed Shearwaters exhibited a strong affinity for transitional waters, and most Tufted Puffins were also found in transitional waters. Least and Parakeet auklets were found mostly in Bering Sea/Anadyr water, and Parakeet Auklets showed a slight preference over Least Auklets for Coastal water (χ^2 = 9.1, df = 2, P < 0.05). Similarly, a significantly higher proportion of Thick-billed Murres compared with Common Murres foraged in transitional and Bering Sea/Anadyr waters (χ^2 = 17.7, df = 2, P < 0.001).

3.7. Diets and condition of seabirds at Cape Thompson

Murres and kittiwakes collected at Cape Thompson in July and August fed predominantly on schooling fishes, of which Arctic cod was most important by frequency of occurrence or percentage wet weight (Table 2). The average (± SD) length of Arctic cod taken by all species was 157 ± 38 mm (n = 202), with an extrapolated average weight of about 31 g. Thick-billed and Common murres also fed frequently on sand lance, saffron cod, and sculpins, but these contributed little to the total mass of food consumed because of their low numbers or relatively small average masses (about 6.7, 23, and 4.8 g, respectively). Thick-billed Murres also fed on invertebrates, and they are probably underrepresented in diets owing to their rapid digestion (Springer et al. 1984). Only kittiwakes consumed herring, which were abundant nearshore in July and early August. Herring consumed by kittiwakes were estimated to be about 200 mm in total length and 100 g in weight (Whitmore and Bergstrom 1983). Kittiwakes had obvious difficulty swallowing such large fish. Herring were apparently too large for murres to handle or swallow, and murres ignored herring schools around Cape Thompson.

The numbers of fish (or otoliths) found in bird stomachs varied markedly throughout the breeding season (Table 3). Arctic cod predominated in diets in early to mid-July, then declined markedly by mid- to late August. Sand lance, saffron cod, and herring were also consumed in smaller quantities. Birds had proportionately more food in

Figure 8
Sea surface temperature-salinity diagram of all waters sampled on surveys in the southeastern Chukchi Sea, and the distribution and abundance of selected seabird species within different water types (see Methods for definition of water types). Species codes: LEAU = Least Auklet, COMU = Common Murre, TBMU = Thick-billed Murre, BLKI = Black-legged Kittiwake, STSH = Short-tailed Shearwater.

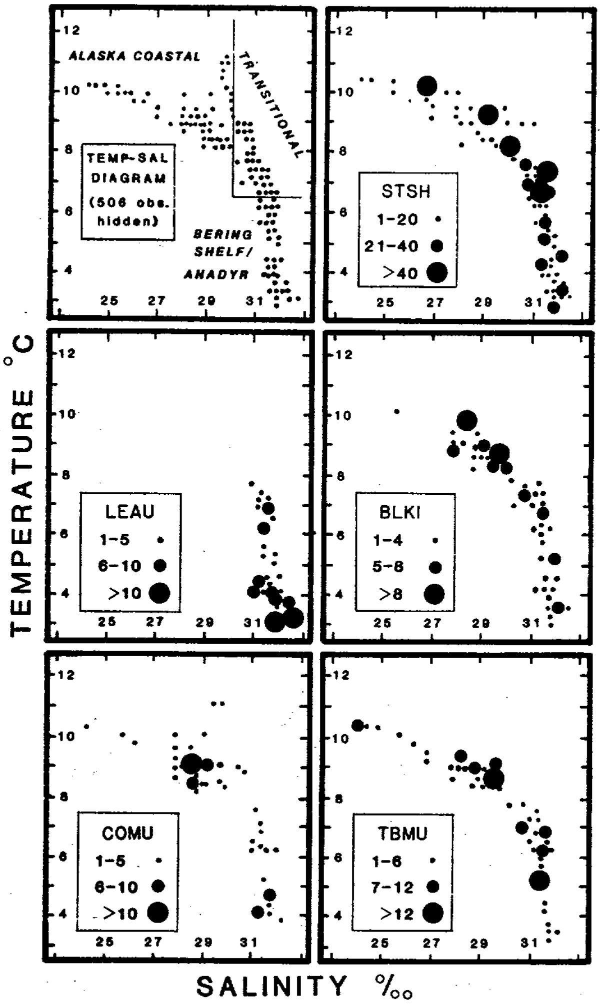
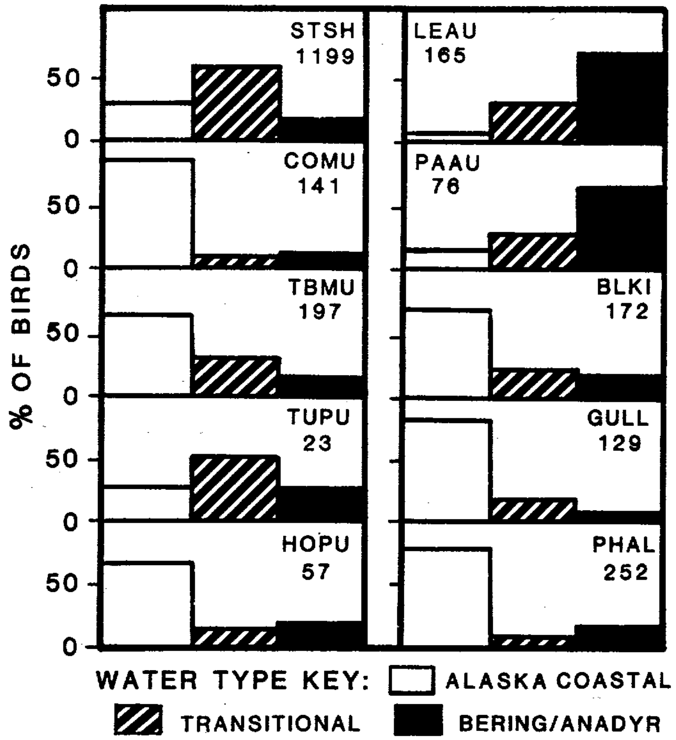


Figure 9
The proportion of seabirds observed in different water types in the southeastern Chukchi Sea (proportions weighted by the total area surveyed in each water type). Species codes: TUPU = Tufted Puffin, HOPU = Horned Puffin, PAAU = Parakeet Auklet, GULL = gull spp., PHAL = phalarope spp.; for other codes, see Figure 8 caption.



their stomachs in July than in August (Table 3), and most empty stomachs were found in August (Table 2).

Murre and kittiwake body masses declined between July and August, although the difference was significant only for male Thick-billed Murres and kittiwakes (Table 4). The body masses of Common Murres, Thick-billed Murres, and kittiwakes (male only) declined by 4, 8, and 11%, respectively. Fat deposits in both murre species increased or remained stable between July and August, whereas kittiwake fat deposits decreased significantly.

4. Discussion

Two oceanographic features of the southeastern Chukchi Sea figured prominently in our study of the distribution and abundance of seabirds and their prey. First, the presence of two distinct water masses (Bering Sea/Anadyr and Alaska Coastal currents) and the front between them resulted in three distinct marine habitats. Second, sea ice disappeared from the area later in 1988 than in any previous year of study (BSF, unpubl. data), and SSTs were about 1–2°C colder than those reported by Fleming and Heggarty (1966) and Coachman et al. (1975).

Below, we consider the influence of these oceanographic conditions in our discussions of:

(1) potential forage fish distribution and abundance;
(2) foraging ecology and distribution of breeding and migrating seabirds; and
(3) the relationship between foraging and breeding success of seabirds at Cape Thompson.

4.1. Forage fish distribution and abundance

It is likely that most of the prey recorded on hydroacoustic surveys were Arctic cod. Extensive trawl surveys conducted throughout the study area in August 1959 revealed that Arctic cod were by far the most abundant and widely distributed fish in the region: numbers caught exceeded those of other common fishes by at least 1–2 orders of magnitude (Alverson and Wilimovsky 1966). There is no indication from predator studies that the forage fish fauna has changed substantially since these trawl surveys were conducted (Divoky 1978; Lowry and Frost 1981; Springer et al. 1984; Bradstreet et al. 1986; this study), and there are no fisheries for Arctic cod. A variety of flatfishes (Pleuronectidae) and sculpins are common in the area, but most of these demersal fishes would not have been detected by our hydroacoustic surveys. However, other common pelagic species, such as capelin (offshore) and saffron cod (inshore), may have contributed to our estimates of fish density. As those species are also consumed by seabirds, are similar in size to Arctic cod, and have similar target strengths (Foote 1987; Rose and Leggett 1988), our estimated forage fish densities were probably not biased much by using Arctic cod target strengths. Indeed, "fish with swimbladders appear to constitute a single class with respect to target properties" (Thorne 1983).

Table 2
Occurrence of major taxa in diets of Thick-billed Murres (TBMU), Common Murres (COMU), and Black-legged Kittiwakes (BLKI) at Cape Thompson in summer 1988[a]

	TBMU		COMU		BLKI	
Parameter	n	%	n	%	n	%
Number examined	46	(100)	14	(100)	18	(100)
Number empty	15	(33)	1	(7)	2	(11)
Frequency of invertebrates	5	16	0	0	3	19
Frequency of fish	30	97	13	100	14	88
Number of individuals						
Arctic cod	125	78	58	89	22	71
Saffron cod	5	3	2	3	0	0
Sculpins	4	2	1	2	0	0
Herring	0	0	0	0	5	16
Sand lance	18	11	1	2	0	0
Unidentified fish	3	2	2	3	1	3
Shrimps	2	1	0	0	0	0
Amphipods	3	2	0	0	0	0
Gastropods	1	1	0	0	3	10
Estimated wet weight						
Arctic cod	4527	94	1429	94	524	51
Saffron cod	99	2	62	4	0	0
Sculpins	16	<1	8	<1	0	0
Herring	0	0	0	0	500	48
Sand lance	126	3	2	<1	0	0
Unidentified fish	30	<1	20	1	10	1
Shrimps	<1	<1	0	0	0	0
Amphipods	<1	<1	0	0	0	0
Gastropods	1	<1	0	0	3	<1

[a] Values in parentheses are the percentage of all stomachs examined. Remaining percentages are the percent number or weight among birds with identifiable prey remains.

Table 3
Mean (± SE) numbers of fishes in the diets of murres and kittiwakes at Cape Thompson, 1988

	Date		
Species	6–12 July	11 August	27 August
Thick-billed Murre (n)	(19)	(15)	(12)
Arctic cod	6.1 ± 2.0	0.53 ± 0.27	0.17 ± 0.11
Saffron cod	0.21 ± 0.12	0	0
Sand lance	0	0	1.5 ± 0.71
All fish	6.3 ± 1.2	0.73 ± 0.28	1.9 ± 0.72
Common Murre (n)	(8)	(6)[a]	
Arctic cod	6.4 ± 0.75	1.2 ± 0.83	
Saffron cod	0.13 ± 0.13	0.17 ± 0.17	
Sand lance	0	0.17 ± 0.17	
All fish	6.5 ± 0.65	2.2 ± 0.79	
Black-legged Kittiwake (n)	(12)	(6)[a]	
Arctic cod	1.4 ± 0.47	0.83 ± 0.54	
Herring	0.33 ± 0.14	0.17 ± 0.17	
All fish	1.8 ± 0.43	1.0 ± 0.52	

[a] Includes one bird collected on 27 August.

Observations from Cape Thompson and at sea indicate that herring have migrated out of the area by late August. Sand lance are a relatively minor component of the fish fauna in August (Alverson and Wilimovsky 1966) but in many years constitute an important part of piscivorous seabird diets (Springer and Roseneau 1978, 1979; Springer et al. 1984). Our observations at sea and from the colony at Cape Thompson, together with the scarcity of sand lance (and capelin) in seabird diets compared with previous years, suggest that sand lance (and capelin) were uncommon in 1988, possibly because the water temperatures were colder than normal (Springer et al. 1984; Piatt 1987).

Pelagic fish were widely dispersed on our surveys in late August. Average densities estimated for inshore ($0.73\ g \cdot m^{-3}$) and offshore ($0.073\ g \cdot m^{-3}$) areas correspond to fish concentrations of less than about one fish per 100 m^3. Even some of the dense aggregations observed inshore included only about 30–300 fish per 100 m^3. These estimates were corroborated by visual inspection of echogram traces. Owing to higher densities inshore, the total biomass (6200 mt) of fish inshore (in the 1170-km^2 area in which survey No. 11 was conducted) was higher than the total biomass (5080 mt) offshore (in the 2320-km^2 area offshore circumscribed by survey No. 10). Consistent with these observations, Alverson and Wilimovsky (1966) caught fewer Arctic cod (mean ± SE, 58 ± 12, n = 28) during standardized offshore trawls (outside the 30-m contour) than on trawls conducted inshore (217 ± 144, n = 7). As indicated by variance/mean ratios (I′) calculated for those trawls, Arctic cod were more highly aggregated inshore (I′ = 669) than offshore (I′ = 76).

Thus, it appears that, in August, fish were more abundant and tended to aggregate more in Coastal waters than in offshore Bering/Anadyr waters. As indicated by the negative correlation with SST gradients on the surveys over the front, fish avoided the core of transitional (frontal) waters between the two currents. Furthermore, pelagic fish in stratified Bering/Anadyr waters were concentrated in midwater above the 2°C isotherm, whereas inshore they formed dense concentrations down to the bottom (possibly because bottom water temperatures were much warmer inshore). Fish in Coastal waters also tended to aggregate near the front with Bering/Anadyr water, as indicated by the positive correlation between fish density and SST gradients on the inshore survey.

Table 4
Body weight (g) and mean indices of subcutaneous (Sub-fat) and mesenteric (Mes-fat) body fat content of Thick-billed Murres (TBMU), Common Murres (COMU), and Black-legged Kittiwakes (BLKI) collected at Cape Thompson

		Male + female			Male			Female			Sub-fat		Mes-fat	
Species	Date	Wt.	SE	n	Wt.	SE	n	Wt.	SE	n	Mean	SE	Mean	SE
TBMU	6–8 Jul.	1037	15	19	1051	16	16	963	14	3	1.5	0.1	0.9	0.1
TBMU	11 Aug.	952	15	15	972	18	9	921	21	6	2.2	0.1	1.3	0.1
TBMU	27 Aug.	946	15	12	949	22	8	941	9	4	2.1	0.2	1.3	0.1
COMU	8 Jul.	1030	24	8	1007	28	3	1044	32	5	2.0	0.0	1.0	0.0
COMU	11 Aug.[a]	985	28	6	990	55	3	980	9	3	2.2	0.2	1.0	0.0
BLKI	8–12 Aug.	508	18	11	545	20	6	452	18	6	2.3	0.2	2.1	0.2
BLKI	11 Aug.[a]	485	16	4	485	16	4	—	—	—	1.4	0.2	1.6	0.2
Overall means[b]														
TBMU		985	11	46	1005	13	33	937	12	13				
COMU		1011	19	14	998	31	6	1020	23	8				
BLKI		495	15	16	521	16	10	452	18	6				

[a] Includes one bird collected on 27 August.
[b] Thick-billed Murre males significantly heavier than females on 6–8 July ($t = 4.14$, df = 17, $P < 0.01$) and over all dates combined ($t = 3.84$, df = 44, $P < 0.01$). Male kittiwakes heavier than females ($t = 3.46$, df = 10, $P < 0.01$). Male Thick-billed Murres ($t = 4.3$, df = 23, $P < 0.001$) and kittiwakes ($t = 2.34$, df = 8, $P < 0.05$) significantly lighter between July and August. Significant increase in fat content of Thick-billed Murres (Sub-fat: $t = 4.95$, df = 32, $P < 0.001$; Mes-fat: $t = 2.83$, df = 32, $P < 0.001$) and decrease in fat content of kittiwakes (Sub-fat: $t = 3.18$, df = 15, $P < 0.01$; Mes-fat: $t = 1.76$, df = 15, $P > 0.05$) between July and August. All other comparisons nonsignificant using two-tailed t-test.

4.2. Foraging ecology and distribution of seabirds

As previous investigators (Swartz 1967; Divoky 1978; Drury et al. 1981) have done, we found that murres, shearwaters, and kittiwakes were the most abundant and widely distributed seabirds in the southeastern Chukchi Sea in late summer. Swartz (1966, 1967) and Springer et al. (1984) noted the importance of the Bering Sea and Alaska Coastal currents, and the front between them, in determining the distribution of seabirds. On the basis of those studies and our own findings, we have reached the following conclusions about seabird foraging ecology in the southeastern Chukchi Sea.

All of the dominant seabirds breeding at Cape Thompson are piscivorous, and most were found within coastal waters where fish densities were highest. Their relative distribution between Alaska Coastal, transitional, and Bering Sea waters was consistent with the known dietary habits of each species. Murre numbers were positively correlated with fish densities. Common Murres feed almost exclusively on dense schools of pelagic fish (Springer et al. 1984; Piatt et al. 1988; Piatt 1990), and they showed a greater affinity for Alaska Coastal water than any other species. Thick-billed Murres also feed heavily on fish but generally have a more diverse diet than Common Murres (Springer et al. 1984; Piatt et al. 1988). Accordingly, a higher proportion of Thick-billed Murres foraged in transitional and Bering Sea waters compared with Common Murres. Transitional waters could possibly have a greater diversity of prey types than adjacent Bering Sea or Coastal waters, because both water masses and associated prey contribute to the composition of transitional waters. Furthermore, upwelling or downwelling at the front may serve to bring prey to the surface or concentrate prey in surface slicks (Brown 1980; Brown and Gaskin 1988; Schneider et al. 1990). Similarly, Horned Puffins, kittiwakes, and Glaucous Gulls, which feed heavily on pelagic fish but also have more diverse diets than Common Murres (Swartz 1966; Springer et al. 1984), were more often found in transitional and Bering Sea waters.

Five other common seabirds that did not breed in the Cape Thompson area were observed on our surveys. Least Auklets foraged widely over stratified Bering Sea waters and were concentrated on the Bering Sea side of the front off Cape Thompson. Least Auklets have a strong preference for Bering Sea/Anadyr copepods (e.g., *Neocalanus plumchrus*) (Bédard 1969; Hunt et al. 1990), and zooplankton are much more abundant in Bering Sea waters off Cape Thompson than in adjacent Coastal waters (English 1966). Vertical stratification and upwelling may be important mechanisms for concentrating zooplankton exploited by Least Auklets (Hunt et al. 1990). Parakeet Auklets have more diverse diets than Least Auklets (Bédard 1969), and they were more widely distributed among water types. Short-tailed Shearwaters and Tufted Puffins feed on a variety of prey, including fishes, euphausiids, shrimp, squid, and other invertebrates (Hunt et al. 1981), and shearwaters exhibited a stronger affinity for transitional waters than other species. Shearwaters (including Sooty Shearwater *Puffinus griseus*) are often associated with fronts (Schneider 1982; Briggs et al. 1987). Phalaropes (of which 91% were identified as Red Phalaropes) were one of the most abundant seabirds we encountered, and most were found on the Alaska Coastal side of the front north of Point Hope. Phalaropes forage on planktonic prey that accumulate in surface slicks near convergent fronts (Brown and Gaskin 1988).

4.3. Foraging and breeding success of seabirds at Cape Thompson

Perhaps the most interesting question to be asked about the fish densities we observed is: Were they sufficient to support seabirds at the end of their breeding season at Cape Thompson in 1988? Forage fish densities near seabird colonies typically vary a lot during the course of summer, usually reaching a peak during midsummer when chicks are hatching and declining towards the end of the breeding period (Safina and Burger 1985; Piatt 1987, 1990). Except for a few schools found inshore, where densities reached 10–100s $g \cdot m^{-3}$, fish densities were low (0.1–10s $g \cdot m^{-3}$) in late August throughout the study area and especially near Cape Thompson. Fish densities were undoubtedly much higher in July when Arctic cod form large, dense schools along the retreating ice edge and nearshore (Lowry and Frost 1981; Springer et al. 1984; Bradstreet et al. 1986). Accordingly, the frequency of cod in murre and kittiwake stomachs at Cape Thompson declined by about an order of magnitude between July and August. Although a decline in fish availability at the end of the breeding season may be a normal experience for seabirds at Cape Thompson (and elsewhere), the frequency of fish in murre and kittiwake stomachs in August 1988 was much lower than in several previous years of study (Springer et al. 1984).

Murres and kittiwakes were affected differently by the low forage fish densities we observed in August 1988. Although murres lost weight between July and August, their body fat stores remained stable or increased, and their breeding success (approximately 50%: BSF, unpubl. data) was normal for these species in Alaska (Piatt et al. 1988). In contrast, kittiwakes lost weight and fat stores in August and experienced the second lowest level of breeding success (about 12%: BSF, unpubl. data) recorded for Cape Thompson in eight years. The marked difference between murres and kittiwakes in body condition and breeding success may have resulted from both the inability of surface-feeding kittiwakes to exploit forage fish below the ocean surface and the scarcity of sand lance, which often comprise the bulk of kittiwake diets in August (Springer et al. 1984). Cold water temperatures probably inhibit the northward migration of sand lance to Cape Thompson (Springer et al. 1984), and that may have accounted for their scarcity in 1988.

5. Summary

As in other oceanic regions (Brown 1980; Schneider 1982; Haney 1986; Briggs et al. 1987), we found that seabird foraging habitats in the southeastern Chukchi Sea were delineated by oceanographic features that could be characterized by gradients in water temperature and salinity. Forage fish school density, abundance, and distribution (vertical and horizontal) varied considerably between habitats. These variations appeared to determine where some seabird species foraged and influenced their foraging and breeding success.

The use of hydroacoustics to study seabird prey below the ocean surface offers great promise for helping to define marine habitats, for studying ecological segregation of seabirds at sea, and for bridging the gap in knowledge between the biology of seabirds at their colonies and at sea. This is particularly true for Arctic and sub-Arctic waters where subsurface foragers dominate seabird communities and pelagic prey are easily detected.

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Appendix 1
Species and numbers of marine birds and mammals observed on all surveys in the southeastern Chukchi Sea (in order of abundance)[a]

Common name	Scientific name	No.
Murre spp.		8237
Thick-billed Murre	*Uria lomvia*	680
Common Murre	*Uria aalge*	198
Short-tailed Shearwater	*Puffinus tenuirostris*	1292
Black-legged Kittiwake	*Rissa tridactyla*	684
Eider spp.		647
King Eider	*Somateria spectabilis*	2
Phalarope spp.		271
Red Phalarope	*Phalaropus fulicaria*	91
Red-necked Phalarope	*Phalaropus lobatus*	8
Least Auklet	*Aethia pusilla*	165
Glaucous Gull	*Larus hyperboreus*	131
Horned Puffin	*Fratercula corniculata*	101
Parakeet Auklet	*Cyclorrhynchus psittacula*	76
Tufted Puffin	*Fratercula cirrhata*	23
Brant	*Branta bernicla*	20
Northern Fulmar	*Fulmarus glacialis*	14
Jaeger spp.		15
Pomarine Jaeger	*Stercorarius pomarinus*	11
Parasitic Jaeger	*Stercorarius parasiticus*	3
Arctic Tern	*Sterna paradisaea*	9
Pacific Loon	*Gavia pacifica*	3
Oldsquaw	*Clangula hyemalis*	2
Sabine's Gull	*Xema sabini*	2
Herring Gull	*Larus argentatus*	2
Crested Auklet	*Aethia cristatella*	2
Common Loon	*Gavia immer*	1
Pelagic Cormorant	*Phalacrocorax pelagicus*	1
Pigeon Guillemot	*Cepphus columba*	1
Gray Whale	*Eschrichtius gibbosus*	24
Humpback Whale	*Megaptera novaeangliae*	1
Spotted Seal	*Phoca largha*	1

[a] For survey effort, see Table 1.

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